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The Value of Myology as an Aid in the Classification of Animals.

BY

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THE opinion of most systematists, and of anatomists too, is, I believe, that the study of muscles is not of much value for classificatory purposes; first, because muscles are liable to a good deal of individual variation; secondly, because they are often difficult to identify by those who are not specially working at them; and thirdly, because of the impression that the arrangement of the muscles depends largely on the habits and mode of life of the animal to which they belong.

With regard to the first objection, that muscles are very variable, Dobson in 1884² stated his opinion that the muscles of the lower wild mammals do not show anything like the same proportion of abnormalities that are met with in man. This opinion my own experience bears out, although I am bound to confess that variations do occur fairly often. Still, if several muscles are taken, the risk of any serious inconvenience from this source is small.

The second objection is not a very serious one. Nobody wishes to lay any stress on slight differences of size or attachment, but rather on the presence or absence of muscles, and on the shifting of their attachments from one bone to another.

The third question, namely, the extent to which muscles vary with the mode of life of their possessor, is the one which I wish to consider most fully. I propose to put forward certain facts gathered from a study of the muscles of the great Order, Rodentia, an Order which contains climbing, swimming, digging, running, and, in a sense, flying forms. Thus I hope to substantiate my contention, that the muscles of an animal tell much more about its classificatory position and the habits of its ancestors than about its own present habits.

One of the most interesting points in the myology of rodents has already been discussed by Dobson³; it is the relation which the two long flexors of the sole bear one to the other. These two flexors are spoken of in human anatomy as the "flexor longus hallucis," which

¹ Paper read before Section D of the British Association, Ipswich, 1895.

² *Journ. Anat.*, xix., p. 16.

³ *Journ. Anat.*, xvii., p. 142.

rises from the fibula, and the "flexor longus digitorum," which comes from the tibia. As these names are quite misleading when applied to the lower animals, Dobson has very wisely suggested the terms "flexor fibularis" and "flexor tibialis," respectively. In the whole of the sub-order of the Hystricomorpha, or porcupine-like rodents, these two tendons join in the sole; in the squirrel group, or Sciromorpha, they do not join, but the flexor tibialis is inserted separately into one of the tarsal bones. In a specimen of the flying squirrel (*Pteromys oral*), I found the flexor tibialis dividing, one half joining the flexor fibularis, while the other had the insertion usual in Sciromorpha. The mouse-like rodents (Myomorpha) are placed by the systematists nearer to the squirrels than to the porcupines; consequently one is not surprised that the long tendons are arranged as in the former animals. I have, however, been somewhat interested to find two exceptions, the bamboo rat (*Rhizomys badius*) and the pocket mouse (*Heteromys longicaudatus*). One of the most curious things is that the jerboas have the tendons united, and in this respect approach the Hystricomorpha. Dobson lays the greatest stress on the value of these tendons as an indication of natural position among the rodents; but I am inclined to think that they should be used carefully and only in conjunction with other muscles. It is largely owing to the arrangement of these tendons that Dobson claims a place for the Dipodidæ among the Hystricomorpha, but I have just been able to show that among the Myomorpha a similar arrangement exists in *Rhizomys* and *Heteromys*. To this question of the position of the Dipodidæ I return later.

Another noteworthy muscle is the "sterno-scapularis." This consists of two parts: one running from the first rib, at its junction with the sternum, to the clavicle, and corresponding entirely to the human subclavius; the other reaching from the clavicle over the supraspinatus muscle to the spine of the scapula. These two parts are often continuous beneath the clavicle, and are supplied by the same nerve. The first part, the "subclavius," is always present; the second part, the "scapulo-clavicularis," is never found in the Sciromorpha, but was present in every specimen of the Hystricomorpha examined, with the exception of the jerboas, whose position is still unsettled. The hare-like rodents (Lagomorpha), as one would expect, resemble the Hystricomorpha in the presence of the muscle, while the Myomorpha approach the Sciromorpha in wanting it. Among this latter group, however, are two exceptions in which it is present; namely, the African mole-rats, *Bathyergus* and *Georychus*. The former of these has already been suspected of affinities with the Hystricomorpha on account of the structure of its mandible, and it is interesting to notice how the muscle seconds the testimony of the bone. The action of this muscle must be to lessen the angle between the clavicle and scapula, and so to make the glenoid cavity face more downwards. This action is, doubtless, most useful in digging, and it

may be urged that the presence of the muscle in these subterranean forms depends more on their mode of life than on their relationship. Against this view I would urge the case of the mole-rat, *Rhizomys*, which is also subterranean, yet which does not possess the muscle, and also the fact that the muscle is found in all the Hystricomorpha, including animals such as the tree-porcupines, the agoutis, and the cavies. It is interesting to turn aside for a moment to speculate on the methods by which this muscle might appear or disappear. Only two occur to me: first, that it is a delamination from the subjacent supraspinatus; secondly, that it has been formed by the conversion into muscle of the fascia over the supraspinatus, by the encroachment of fibres from the subclavius. In favour of the latter, and against the former, hypothesis are the facts that the muscle is often continuous with the subclavius, and that it is supplied by the same nerve and not by the suprascapular nerve, which supplies the supraspinatus.

Both the muscles already selected as examples tend to show that the myomorphine arrangement is more closely allied to the sciuromorphine than to the hystricomorphine and lagomorphine. It is not difficult to find other examples of this. For instance, the small transverse mandibular muscle, which unites the two halves of the lower jaw close to the symphysis, is present in the Sciromorpha and Myomorpha, absent in the Hystricomorpha and Lagomorpha.

The scapulo-clavicularis is an instance of a muscle which is not found at all in the Sciromorpha, is always present in the Hystricomorpha and Lagomorpha, and is very rarely seen in the Myomorpha. I will next give instances of muscles which are present in the more generalised squirrel group, and are gradually lost as we ascend to the more specialised. The above-mentioned transverse mandibular muscle is one instance of this; another is the omo-hyoid, which is always present in the Sciromorpha and Myomorpha, but is absent in certain families of the Hystricomorpha, such as the Chinchillidæ, Dasyproctidæ, and Caviidæ. In the Hystricidæ it is absent in the ground-porcupines *Hystrix* and *Atherura*, but present in the tree-porcupines *Sphingurus* and *Erethizon*. In the Lagomorpha the muscle is absent in the hare and rabbit.¹ The presence of the omo-hyoid in the tree-porcupines and its absence in the ground-porcupines may certainly be regarded as an instance of change of musculature accompanying change of habits, more especially as there is, so far as I am aware, no arboreal rodent which does not possess an omo-hyoid. My object, however, is not to prove that this never occurs, but rather to show that, in spite of it, many muscles vary very constantly with the relationships of the animals that possess them, and may be advantageously considered in classification.

Another muscle on which I am inclined to lay a good deal of

¹ I have, unfortunately, never had the opportunity of dissecting a *Pica*, the other genus of this suborder, nor can I find any account of its myology.

stress is the "supinator longus," a muscle that tends to disappear on very slight provocation. It is present in all the Sciuroomorpha that I have examined, with the exception of the beaver; that is to say, it is present in the squirrel, the flying squirrel (*Pteromys*), the ground squirrel (*Xerus*), the marmot, and the gopher. I am unable to say whether it is found in the families of the Anomalures and Haplodonts as I have never had an opportunity of dissecting examples of these, and can find no records of such dissections; but there is no doubt that the muscle is a very common one among the generalised squirrel sub-order. In the Myomorpha it is not found at all. Among the Hystricomorpha I have never seen it, but I find an account of it in tree-porcupines, dissected by Mivart¹ and Windle.² In the Lagomorpha it is also absent. It may be said that this is a muscle which depends very much on the climbing habits of its possessor, and in a certain sense this is true; but the point on which I wish to lay stress is that the marmot, which does not climb and is a near relative of the squirrel, has a well-developed supinator, while the tree-porcupine, *Sphingurus*, has no trace of it—indeed, in Windle's specimen of *Erethizon* it was quite rudimentary. If further evidence be needed that its presence does not necessarily imply climbing, one may point to the fact that it is present in the jerboas, three different species of which I have examined.

The supinator longus is also valuable in the Carnivora, for it is present in the Felidæ, Procyonidæ, and Ursidæ, but absent in the Hyænidæ and Canidæ. It is more important, however, to notice its distribution in the rodents; since some authors, even in books of reference, have stated that it is absent in this Order.

It is not only the presence or absence of certain muscles that varies with the classificatory position of animals; the attachments are also valuable. A good instance of this is the "levator claviculæ" or acromio-trachelien; in the Sciuroomorpha and Myomorpha this always rises from the atlas, while in the Hystricomorpha it is most inconstant, in some cases rising from the atlas, and in others from the basioccipital. It will be a good test to pick out those animals in which this change of origin has been effected, and to see whether there is any marked similarity in their mode of life which might account for it. The animals in which I have found the basioccipital origin are the African ground rat (*Aulacodus*) which inhabits cane-brakes, the hutia (*Capromys*) an arboreal form, the coypu (*Myopotamus*) which is aquatic; the ground-porcupines (*Hystrix* and *Atherura*), and the spotted cavy (*Coelogenys*) which are terrestrial forms, as well as three genera of the family of Caviidæ (*Cavia*, *Ceredon*, and *Dolichotis*), all of which are also terrestrial. This list, I think, does not point to the change of attachment being due to any definite change in the animals' mode of life. Hitherto I have only instanced muscles which indicate the sub-order to which the animal belongs; but it would be

¹ Proc. Zool. Soc., 1882, p. 271.

² Journ. Anat., xxii., p. 126.

quite possible to place a specimen in its proper family by referring to the combinations of muscles which are characteristic of that family. For instance, the absence of a scalenus anticus in a hystricomorphine rodent would at once make me suspect that it was a porcupine; if it wanted a peroneus quarti I should suspect it of being a tree-porcupine; and if in addition it had two heads to the biceps cubiti, a well-developed omo-hyoid, and a levator claviculae rising from the atlas, I should feel pretty certain that it was one.

The question which I should expect to be asked, and which, indeed, has been asked, is "What light does myology throw on the position of the Dipodidae?" Dobson¹ says that the only argument for placing them among the Myomorpha is the fact that the tibia and fibula are fused, while in favour of including them in the Hystricomorpha are the united flexors in the sole, the masseter passing through the infraorbital foramen, the external appearance of the ears and muzzle, the armed condition of the penis, and the arrangement of the teeth.

With regard to the fused tendons, I have been able to point out two examples of myomorphine rodents in which these are present. The large size of the infraorbital foramen is a question of degree, since in most myomorphine rodents a small piece of the masseter passes through this opening, and it is only in sciromorphine and lagomorphine rodents that the infraorbital foramen transmits nothing but the nerve. With regard to the classificatory value of teeth, Mivart, in his work on the *Æluroidea*,² has given grounds for not placing much confidence in them, and, for my own part, I cannot help thinking that, unless used with considerable caution, they are apt to mislead. I can add another claim to those which Dobson has given for regarding the jerboas as hystricomorphine, and that is that they have only one head to the biceps cubiti, while every myomorphine rodent that I have looked at possesses two. On the other hand, in addition to the fusion of the leg-bones, which is never seen in the Hystricomorpha, the two halves of the lower jaw move upon one another and are provided with a transverse mandibular muscle; the digastric is arranged on the sciromorphine type described by Kunstler,³ a type which is never found in the Hystricomorpha, but often in the Myomorpha; the scapulo-clavicularis, which I have already laid stress on as being a most constant muscle in the Hystricomorpha, is absent; and the omo-hyoid is present as in all the Myomorpha, while it is often absent in the Hystricomorpha. On the whole, I certainly think that the myology of the jerboas points to their having myomorphine rather than hystricomorphine tendencies, though their many points of difference from both groups might entitle them to subordinal rank, as Dipodomorpha. With regard to the affinities that Dobson believes them to have with the Chinchillidæ, a

¹ Proc. Zool. Soc., 1882, p. 640.

² Proc. Zool. Soc., 1882.

³ Ann. Sci. Nat., ser. 7, t. iv., p. 150.

study of their muscles negatives the idea entirely. In addition to the scapulo-clavicularis and the digastric and transverse mandibular points of divergence, the Chinchillidæ have two heads to the biceps cubiti, the jerboas only one; in the Chinchillidæ the biceps is inserted into both bones of the forearm, in the Dipodidæ only into the ulna; in the Chinchillidæ the omo-hyoid is absent, in the jerboas it is present; in the Chinchillidæ the tibialis anticus rises from the tendon of the extensor longus digitorum as well as from the tibia, in the Dipodidæ it rises only from the tibia. I am pleased to notice that Winge, in his monograph on "The Rodents of Lagoa Santa" (*E. Museo Lundii*, iii., 1888) separates the Dipodidæ from the Hystricomorpha, but for other reasons than those I have brought forward.

In concluding this paper I must admit that I have founded my generalisations on the study of one Order of mammals; but this is partly because I have paid more attention to rodents than to other animals, and partly because a general review of myological literature would far exceed the limits of a paper such as this. My observations on other animals, as well as a study of the literature of the subject, make me think that what is true for one of the largest Orders holds good for the rest. Attention may be directed to a most complete paper by Wilson on the myology of *Notoryctes typhlops* as compared with that of other mammals, in which the following passage occurs¹: "I cannot avoid the conclusion that the structural resemblances in particular to certain members of the order Edentata are not all to be explained as merely the coincidences of somewhat similar functional modifications, but are the enduring evidences of a real if distant morphological kinship." This is practically my own view, and I would urge that certain muscles provide a very good clue to the relationships of animals, the great point being to select the muscles on which reliance is to be placed.

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¹ *Trans. Roy. Soc. S. Austral.*, 1894